

ZOOGEOGRAPHY OF THE PENAEIDAE

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The Penaeidae are tropical stenotherms, mostly inhabiting shallow, silty inshore environments. Their present distribution appears to be largely determined by a combination of geological history, temperature, ocean currents, ocean depths and coastal geography. Penaeids are almost six times more diverse in the Indo-West Pacific Region than in the Western Atlantic, which may be related to continental shelf area or the length of shoreline. Most extant genera probably originated in the Tertiary, and there is evidence that some species have separated within the last 2 million years. Except for a few pelagic and deep-water species, the penaeid populations of the Indo-West Pacific, Eastern Pacific and Western Atlantic Regions are discrete. Within each region, two or more subregions have been defined, supported by cluster analysis of the Indo-West Pacific Region. Reasons for these divisions are discussed, particularly the barriers to penaeid movements from the Indo-Malaysian to the Tropical Australia Subregion. These barriers appear to be primarily deep water and unfavourable currents along the steep northern and southwestern coasts of New Guinea. Possible causes of Southern Hemisphere endemism in the Penaeidae are discussed. Because of the absence of fossil records extinction hypotheses cannot be tested, but the apparent absence of amphitropicality in the family and the limited geographic range of many species suggest that evolution within the Southern Hemisphere can account for the endemism of penaeid species there. The unique genera *Macropetasma* and *Artemesia* could be relicts of Miocene, relatively cool-water populations, but there is no firm evidence to support this. □ *Penaeidae*, *zoogeography*, *tropics*, *endemism*, *temperature*, *ocean currents*, *ocean depths*, *Indo-West Pacific*, *Eastern Pacific*, *Western Atlantic*

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The Penaeidae is the best-known family within the Penaeoidea in the decapod Suborder Dendrobranchiata. The 171 known species within 17 genera (Table 1) are predominantly tropical and subtropical. About 80% of these species usually live in depths of <100 m; the remainder normally either inhabit deeper water (10 *Metapenaeopsis* spp.; most *Parapenaeus* spp.; all *Penaeopsis* spp.) or are pelagic (all *Funchalia* spp. and *Pelagopenaeus*). Many of the deep-water and pelagic species appear to be widely distributed. *Funchalia villosa* and *F. woodwardi*, for example, having been recorded in the Pacific, Atlantic and Indian Oceans. Records of the distribution of these pelagic species are, however, too sparse to discuss their zoogeography, so most of this review is devoted to the better-known shallow-water Penaeidae.

All shallow-water Penaeidae so far investigated have a planktonic larval phase of about 2–3 weeks, followed by inshore or estuarine early juvenile stages (Dall *et al.*, 1990). Most species prefer soft substrates, ranging from mud to sand, but a number — probably around 25% — (mainly *Metapenaeopsis* spp., *Heteropenaeus*,

Trachypenaeopsis), prefer harder substrates such as coral rubble. There is one commensal with corals (*Metapenaeopsis commensalis*).

Both biotic and physical factors are likely to influence the distribution of marine crustaceans such as the Penaeidae. They are subject to considerable predation pressure (Dall *et al.*, 1990); in some areas the population density is high and interactions between species may be important. However, while no studies on the effects of such biotic factors have been made, the physical environment appears to be more important in determining the distribution of penaeids. Their life histories suggest there are four principal factors that may affect their distribution:

1. Temperature. As tropical stenotherms they are restricted to the warmer waters of the world. In lower latitudes, cold winds from continental land masses may cool inshore waters or cause upwelling and thus be barriers to distribution; cold currents from higher latitudes may have a similar effect. Conversely, warm currents may extend the latitudinal range of penaeids along a coast.

2. Oceanic larval advection. The pelagic larval

TABLE 1. Genera of the Penaeidae, the world-wide number of species within each genus and the number of species within each region. IWP, Indo-West Pacific; EP, Eastern Pacific; WA, Western Atlantic; EA, Eastern Atlantic; (P), pelagic, probably present in all oceans; number in parentheses, additional species also present in Western Atlantic.

Genus	Total species	Species per region			
		IWP	EP	WA	EA
<i>Artemesia</i>	1	—	—	1	—
<i>Atypopenaeus</i>	4	4	—	—	—
<i>Funchalia</i>	4	(P)	(P)	(P)	(P)
<i>Heteropenaeus</i>	1	1	—	—	—
<i>Macropetasma</i>	1	1	—	—	—
<i>Metapenaeopsis</i>	49	40	3	5	1
<i>Metapenaeus</i>	25	25	—	—	—
<i>Parapenaeopsis</i>	16	14	1	—	1
<i>Parapenaeus</i>	12	10	—	1	1
<i>Pelagopenaeus</i>	1	—	1	—	—
<i>Penaeopsis</i>	6	5	—	1	(1)
<i>Penaeus</i>	28	14	5	8	1(1)
<i>Protrachypene</i>	1	—	1	—	—
<i>Tanypenaeus</i>	1	—	—	1	—
<i>Trachypenaeopsis</i>	2	1	—	1	—
<i>Trachypenaeus</i>	17	10	5	2	—
<i>Xiphopenaeus</i>	2	—	1	1	—
Total	171	125*	16*	21*	4*

* not including *Funchalia* and *Pelagopenaeus*.

life makes most species susceptible to the influences of currents flowing in unfavourable directions, such as towards higher latitudes or from inshore to offshore.

3. Oceanic deeps. These constitute a barrier for shallow-water species, especially when they are very close inshore or in conjunction with unfavourable currents.

4. Coastal geography. Since most species live in shallow waters, particularly in the early juvenile stages, lack of suitable inshore habitats may constitute a barrier. Thus a desert coastline with high inshore salinities, or a very rocky coast with deep water inshore, may restrict the distribution of some species.

DISTRIBUTION IN TIME

The Penaeidae are an ancient group. Penaeoidea have been recorded in the Mesozoic, back to the Upper Triassic, mostly in various shales of

central Europe, the eastern Mediterranean and Great Britain (Glaessner, 1969), with a few in North America (Herrick and Schram, 1978). Crustacea are, however, poor candidates for fossilisation, particularly the thinner-shelled groups such as penaeids (Bishop, 1986). Further, the normal environmental conditions of penaeids are not conducive to fossilisation because of the presence of numerous scavengers and bioturbation of the sediment by a large burrowing infauna (Plotnick, 1986). Hence the penaeid fossil record is very sparse. The Penaeidae first appear in Jurassic deposits and become more common in the Cretaceous. Most of these earlier Penaeidae became extinct at the end of Mesozoic, *Penaeus* being the only surviving genus. Apart from one *Penaeus* record from India in the early Tertiary, no fossils of more recent origin have been found, so geological evidence of the origins of the remaining 16 extant genera is completely lacking.

The times at which existing genera diverged have therefore to be estimated by other means. Limited data are available from biochemical genetics, supported by palaeogeography (Dall *et al.*, 1990). These authors calculate from genetical data that *Metapenaeus* could have separated from *Penaeus* between the early Tertiary and the Pliocene. The genetic distances within these genera indicate that some present species evolved between the Miocene and the Pleistocene. While estimates of divergence times from biochemical genetics are imprecise, they can be improved by palaeogeographical evidence. Separation of the Atlantic Ocean from the rest of the Tethys Sea by closure of the Mediterranean during the Miocene isolated its warm shallow-water fauna (Por, 1986). Although North and South America were not joined during the Oligocene–Miocene and the present Isthmus of Panama was not established until the Pliocene (White, 1986), physical conditions in the proto-Caribbean and Pacific had begun to differ by the late Miocene (Keigwin, 1978). Fossil evidence also suggests that the two faunas were distinct at this time (Ekman, 1953). Penaeid genera common to the Atlantic, Pacific and Indian Oceans today were presumably in existence before the separation of the Atlantic. These are the shallow-water genera *Penaeus*, *Metapenaeopsis*, *Parapenaeopsis*, *Trachypenaeus* and *Trachypenaeopsis*. On this basis, excluding the deep-water or pelagic genera (*Funchalia*, *Parapenaeus*, *Pelagopenaeus* and *Penaeopsis*), seven may have originated since the Miocene. Thus the combined evidence suggests that the

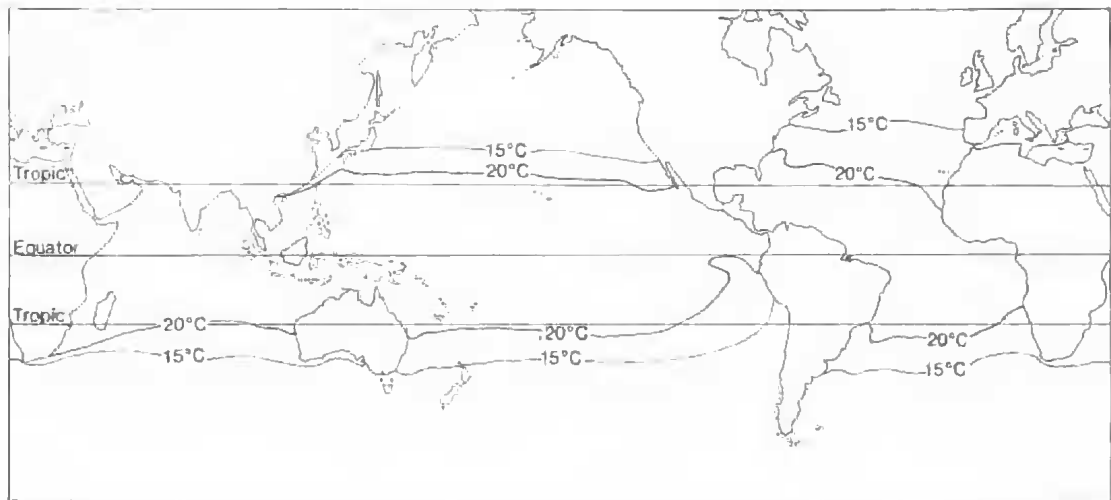


FIG. 1. Location of 20°C and 15°C minimum winter sea surface temperature isotherms. They correspond with the isocrymal lines (coldest 30 consecutive days of the year) of the Northern and Southern hemispheres.

majority of present penaeid genera may have originated in the last 10–15 million years.

as in the Pohai Sea (Angelescu and Boschi, 1959).

WORLD DISTRIBUTION

The Penaeidae are distributed throughout the world, but their latitudinal distribution is limited by temperature. Most species occur within the isotherms of 20°C minimum winter temperatures (Fig. 1). Between the 20°C and 15°C isotherms the number of species falls to about 30% of those within the 20°C isotherms. In these cooler zones, the growth and activity of most species are minimal in winter, but temperatures in summer are usually high enough for them to achieve growth rates comparable with those of fully tropical species. Only two species are abundant outside the 15°C isotherms: *Penaeus chinensis* in the Pohai and Yellow Seas and *Artemesia longinaris* in southeastern South America. Both have adapted to survive temperatures down to about 6°C, but, in addition, the adaptive behaviour of *P. chinensis* enables it to cope with the hostile winter environment. It migrates into the deeper waters of the Yellow Sea at the onset of winter and returns to exploit the rapid warming of the shallow waters in spring and subsequent summer temperatures of 25°C (Chang Cheng, 1984). A similar strategy is not available to *Artemesia*, as water temperatures in the southern half of its range do not rise above 20°C, but winter temperatures are not as severe

REGIONAL DISTRIBUTION

Ekman (1953) divided the shallow, warm-water marine faunas of the world into Indo-West Pacific, Eastern Pacific, Western and Eastern Atlantic Regions. This classification has been followed by Briggs (1974) for various taxonomic groups and by Abele (1982) for Crustacea. The Atlantic is clearly separated from other oceans by the Americas and the Afro-European landmasses, and the deep ocean separates the Atlantic into eastern and western faunas. The Eastern Pacific fauna is separated from the rest of the Pacific by a wide expanse of deep ocean, containing very few islands. Eastward movement of warm-water planktonic larvae is discouraged by the westward Equatorial Current, which is fed in this region by cold currents flowing towards the equator along the west coasts of North and South America. Only species with an exceptionally long larval life can be transported eastward from the Central Pacific (Scheltens, 1988). The fauna of the Eastern Pacific Region does, however, have some affinities with that of the central Western Atlantic, as the final separation of the two oceans did not occur until the early Pliocene and twin species are common (Ekman, 1953). Examples in the Penaeidae are *Trachypenaeus pacificus* : *T. similis* and *Xiphopenaeus riveti* : *X. kroyeri*

(western and eastern coasts of the Isthmus, respectively).

The remainder of the Pacific is not separated zoogeographically from the Indian Ocean and the two are usually grouped together as the Indo-West Pacific Region. Springer (1982), from a study of shallow-water fishes, proposed that the Pacific Plate should be designated as a separate region, but this is not supported by the distribution of corals and echinoderms (Ekman, 1953), nor by that of the Penaeidae (Dall *et al.*, 1990).

Although the number of penaeid genera in the Indo-West Pacific and Western Atlantic Regions is similar, there is great disparity in the number of species (Table 1). Excluding *Funchalia* and *Pelagopenaeus*, the Indo-West Pacific contains 73% of known species, compared with 12% in the Western Atlantic. Abele (1982) found similar ratios for other decapod Crustacea (Portunidae, Parthenopidae, *Sesarma* spp. and *Alpheus* spp.). He also notes that the ratios are due to the large number of congeneric species in the Indo-West Pacific, rather than an increase in the number of genera. Abele (1982) discusses several hypotheses to account for this. On a small scale there is a positive correlation between habitat complexity (e.g. sandy beaches, sand-mud beaches, mangroves, corals and rocky intertidal) and crustacean species diversity, but this does not appear to be valid for zoogeographical regions. It would also be unlikely to apply to the Penaeidae, which occupy similar habitats both latitudinally and longitudinally. Briggs (1974) suggests that the number of species of tropical shallow-water marine animals is directly correlated with continental shelf area. Abele (1982) obtained a positive linear correlation between continental shelf area and numbers of warm shallow-water marine crustacean species in the four major regions. He also obtained a positive log-log relationship between Caribbean island perimeter and number of marine shrimp species (penaeids and carids). Shoreline length may be the reason for the higher penaeid species diversity in the Indo-West Pacific, as the factors that tend to isolate penaeid populations are related to the shoreline.

SUBREGIONS

There are considerable differences in geographical ranges in the Penaeidae, both between and within genera (Dall *et al.*, 1990). Thus the most ancient genus *Penaeus* is, with few exceptions, the most widely ranging. *Penaeus japonicus*, *P. latisulcatus*, *P. marginatus*, *P. monodon*

and *P. semisulcatus* have been recorded in most of the warmer waters of the Indo-West Pacific. In the Eastern Pacific, all *Penaeus* species are found in both subregions, while in the Western Atlantic they extend through at least two subregions, with *P. notialis* occurring on both sides of the Atlantic. The deeper water genera *Parapenaeus* and *Penaeopsis* are also wide ranging, but generally less so than *Penaeus*. The remaining genera are mostly more restricted in range, about 50% of all penaeid species being endemic to one or two subregions. (Some species within these genera with an apparent wide range, such as *Metapenaeopsis mogiensis* and *M. hilarula*, may be complexes of species, A. Crosnier, pers. comm.).

Dall *et al.* (1990) define and discuss penaeid subregions within each of the regions. They used the distribution of species with a restricted range, particularly those endemic to a particular area, to define subregions. Geography and temperature data were also taken into account. These were confirmed for the present study for the Indo-West Pacific Region by cluster analysis of the presence-absence data of all species on the basis of euclidean distance with group average hierarchical clustering (Fig. 2). Bray-Curtis group average hierarchical clustering gave similar groupings, but with Southeast and Southwest Australia separated from the other subregions and closest to the West Pacific. (Reliable cluster analyses for the subregions defined by Dall *et al.* (1990) for the Eastern Pacific and Atlantic were

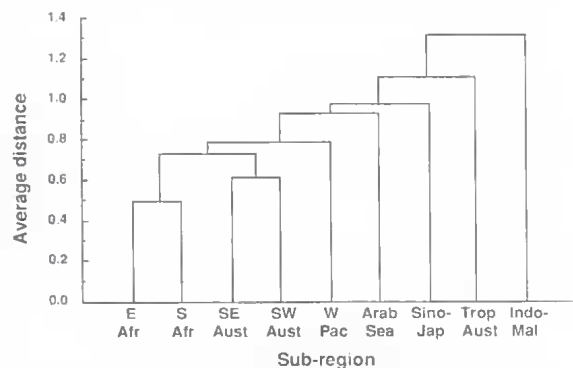


FIG. 2. Group average hierarchical cluster analysis of Indo-West Pacific Subregions, using presence-absence data of all species, based on euclidean distance. Abbreviations: E Afr, East African; S Afr, South African; SE Aust, Southeast Australian; SW Aust, Southwest Australian; W Pac, West Pacific Oceania; Arab Sea, Arabian Sea; Sino-Jap, Sino-Japanese; Trop Aust, Tropical Australian; Indo-Mal., Indo-Malaysian.

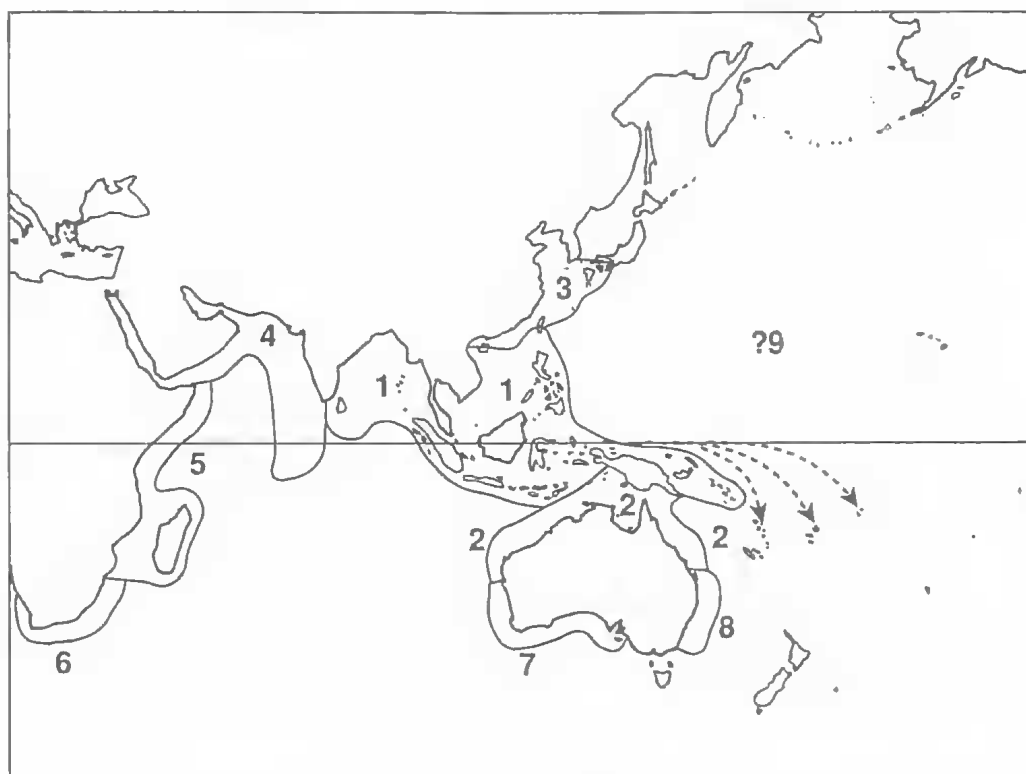


FIG. 3. Subregions of the Indo-West Pacific Region. 1, Indo-Malaysian; 2, Tropical Australian; 3, Sino-Japanese; 4, Arabian Sea; 5, East African; 6, South African; 7, Southwest Australian; 8, Southeast Australian; 9, Pacific Oceania; arrows, extension of Malay-Indonesian Subregion (see text for definitions).

not feasible because of the paucity of species in these areas).

INDO-WEST PACIFIC SUBREGIONS (Fig. 3; Table 2).

1. *Indo-Malaysian*. This is defined in the south by the oceanic deeps off southern Indonesia, which extend into the Timor Sea, to the west of the Aru Islands, coming close inshore at the neck of West Irian. To the east, oceanic deeps and westward equatorial currents form a major barrier, while to the north falling temperatures close off the subregion. There is no obvious barrier in the west, the shallow coastal waters of the Straits of Malacca running without apparent interruption through the Bay of Bengal. However, there is a steady decrease in the diversity of penaeid species diversity from Malaysia to the Bay of Bengal (Dall *et al.*, 1990), as in other faunas (Ekman, 1953). Dall *et al.* (1990) suggest that unfavourable currents, plus the strongly monsoonal climate of India may restrict the westward

movement of penaeids. The southern tip of India has been arbitrarily selected as the western boundary of this subregion.

2. *Tropical Australia*. This subregion extends from the southern coast of New Guinea to the 20°C winter isotherm on the east and west coasts of Australia. The significance of the barriers to the northeast and northwest are discussed in detail below.

3. *Sino-Japanese*. The southern boundary is defined by the 20°C isotherm. The diverse fauna of the Gulf of Tonkin and southern China decreases sharply to the north due to cold continental influences, but the Equatorial Current runs offshore to the northeast, raising the minimum winter temperature in the Sea of Japan and giving this area a large and distinctive penaeid fauna.

4. *Arabian Sea*. This subregion, from the southern tip of India to Cape Guardafui at the entrance

TABLE 2. Total number of species and endemic species in the subregions of the Indo-West Pacific Region. Indo-Mal. Indo-Malaysian; Trop Aust. Tropical Australia; Sino-Jap. Sino-Japanese; Arab Sea. Arabian Sea; E Afr. East Africa; S Afr. South Africa; SW Aust. Southwest Australia; SE Aust. Southeast Australia; O. Pacific Oceania.

	Indo-Mal.	Trop Aust.	Sino-Jap.	Arab Sea	E Afr.	S Afr.	SW Aust.	SE Aust.	O
Total species	84	52	36	38	20	15	8	8	20
Endemic species	22	13	10	3	2	1	2	3	2

to the Red Sea, has extensive arid coastlines; the hypersaline inshore waters and cold continental winter winds probably act as barriers to less adaptable species. The Red Sea is usually treated as a separate subregion because of its distinctive fauna (Ekman, 1953; Briggs, 1974), but the penaeid fauna differs only in having fewer species and has therefore been included in this subregion.

5. *East African Coast*. This extends from Cape Guardafui to Durban. Briggs (1974) regards the coast from the Gulf of Iran to the southern tip of Africa as one subregion, but the East African Coast appears to support a more diverse and possibly larger penaeid population than the Arabian Sea (Crosnier, 1965). Neither the northern nor the southern boundaries are well defined, but there is a drop in species diversity around the latitude of southern Madagascar.

6. *South Africa*. This subregion could be included in East Africa, except for the appearance of *Mucropetasma africanus* at Durban. This species becomes common on the south coast, west of Algoa Bay, where other penaeid species are rare, and is unique in that it extends northward along the west coast of southern Africa from Cape Town to Swakopmund, in the cool waters derived from the Benguela Current.

7. *Southwestern Australia*. The 20°C isotherm defines the northern boundary of this subregion, which extends across southern Australia because of the influence of the warm southerly Leeuwin Current. There are two endemic species: *Metapenaeopsis fusca* and *M. lindae*.

8. *Southeastern Australia*. The 20° C and 15° C isotherms define the northern and southern limits of this subregion. It has three endemic species, *Penaeus plebejus*, *Metapenaeus ben-nettae* and *M. macleayi*; the first two appear to be siblings of widely distributed species.

9. *Pacific Oceania*. The penaeid population of this subregion appears to be mostly an extension of the Indo-Malaysian fauna; it is therefore doubtful that it is a valid penaeid subregion (indicated by the query in Fig. 3). Two endemic species have been identified: *Metapenaeopsis tarawensis* and *M. commensalis*, both inhabitants of coral reefs and the latter a commensal with corals. *M. commensalis* may be more widespread than the published record indicates.

WESTERN ATLANTIC SUBREGIONS (Fig. 4; Table 3.)

The Western Atlantic Region extends from Martha's Vineyard, 43°N to Puerto de Rawson, 43°S. The subregions are:

1. *Caribbean*. This extends from southeast Florida through the Caribbean to Sao Luis, Brazil, but stops at the entrance of the Gulf of Mexico. Geographically this area is analogous to the Indo-Malaysian Subregion of the Pacific. It has the greatest penaeid species diversity (16) within the Atlantic Ocean, with three endemic species (*Tanypenaeus caribeus*, *Trachypenaeopsis mobilispinis*, *Trachypenaeus similis*). The eastern boundary is defined by a marked drop in species diversity, which appears to be due to a strong westward current, plus a monsoonal climate in eastern Brazil.

2. *Eastern Brazil* (Sao Luis to Cabo Frio). The southern boundary at Cabo Frio is caused by a cooler-water coastal northerly current meeting the warm southerly Brazilian Current and diverting it offshore. There are no endemic species, but the species composition is appreciably different from that of the Caribbean.

3. *Gulf of Mexico*. This is defined by *Penaeus aztecus*, *P. duorarum* and *P. setiferus*, which are plentiful in the Gulf of Mexico, but do not extend eastwards into the adjacent Caribbean Sub-

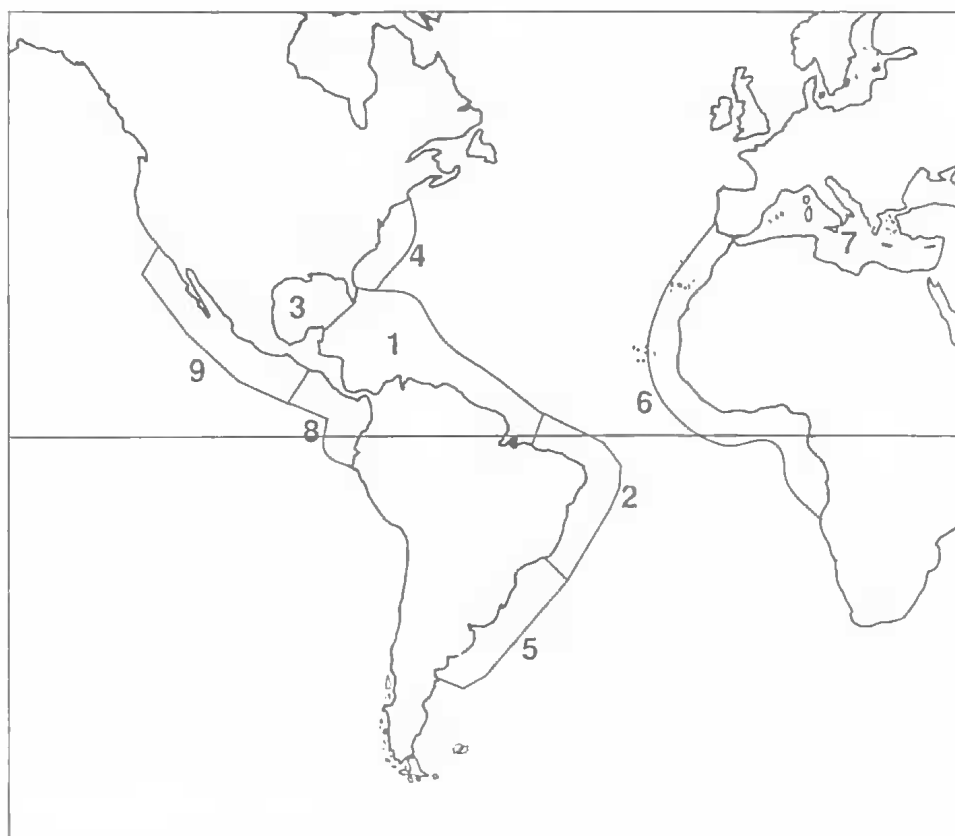


FIG. 4. Subregions of the Western Atlantic, Eastern Atlantic and Eastern Pacific Regions. Western Atlantic: 1, Caribbean; 2, Eastern Brazil; 3, Gulf of Mexico; 4, Eastern USA (Carolinean); 5, Southeast South America. Eastern Atlantic: 6, Eastern Atlantic; 7, Mediterranean Sea. Eastern Pacific: 8, Panamanian; 9, Mexican (see text for definitions).

region. Also, low winter temperatures in the north of the Gulf reduce the species diversity (7 compared with 16 in the Caribbean).

4. *Eastern USA* (Carolinean) (Martha's Vineyard to southeast Florida). Cape Hatteras is the northern limit of abundant penaeid distribution, but there have been records of *Penaeus aztecus* as far north as Martha's Vineyard.

5. *Southeast South America* (Cabo Frio, Brazil to Puerto de Rawson, Argentina). *Penaeus paulensis* and *Artemesia longinaris* are endemic species in this well-defined cooler-water subregion.

EASTERN ATLANTIC SUBREGION

These are shown in Fig. 4 and detailed in Table 3. The Eastern Atlantic Region includes the Mediterranean Sea, usually considered to be a separate zoogeographical area. Also, at least five

Indo-West Pacific species (*Penaeus japonicus*, *P. semisulcatus*, *Metapenaeus monoceros*, *M. stebbingi*, *Trachypenaeus curvirostris*) have migrated through the Suez Canal from the Red Sea (Lessepsian migration) (Gab-Alia *et al.*, 1990). In the Atlantic, penaeids normally extend as far north as about 40°N in Portugal, but in the south the cold Benguela Current limits the distribution to about 16°S in Angola. Thus the subregions are:

6. *Eastern Atlantic* (Lisbon, Portugal, 40°N, to Porto Alexandre, Angola, 16° S).

7. *Mediterranean Sea*. This subregion has only two of the six species found in the Eastern Atlantic, apart from the Lessepsian migrants.

EASTERN PACIFIC SUBREGIONS (Fig. 4; Table 3)

Eastern Pacific Region is reduced latitudinally

TABLE 3. Total number of species and endemic species in the Subregions of the Western Atlantic, Eastern Atlantic and Eastern Pacific Regions. Car, Caribbean; E Br, Eastern Brazil; GoM, Gulf of Mexico; E US, Eastern USA (Carolinean); S SA, Southeastern South America; E A, Eastern Atlantic; Med, Mediterranean Sea; Mex, Mexican; Pan, Panamanian.

	Car	E Br	GoM	E US	S SA	E A	Med	Pan	Mex
Total species	16	11	7	7	4	6	2	12	11
Endemic species	3	0	0	0	2	2	0	5	3

in both the north and south by cold currents flowing towards the Equator; the continental shelf is mostly narrow and there are relatively few islands to support populations of penaeids. Penaeid species composition changes markedly in the El Salvador region, which has been selected as a boundary between the northern and southern subregions. These are:

8. *Panamanian*. El Salvador to Punta Aguja, Peru. The unique *Protrachypene*, *Parapenaeopsis balli* (the only *Parapenaeopsis* in the Western Hemisphere) and three species of *Trachypenaeus* define this subregion.

9. *Mexican*. San Francisco Bay (northern limit of penaeid records) to El Salvador. Here the penaeid diversity is lower than in the Panamanian, with three endemic species *Metapenaeopsis beebei*, *M. kishinouyei* and *Trachypenaeus brevisuturiae*.

BARRIERS TO DISTRIBUTION

Low temperature, and thus latitude, has been mentioned as one of the principal boundaries to penaeid distribution. These boundaries may be modified by warm currents flowing away from the equator, or cold currents flowing towards it. Thus the northern boundaries of the South African, Southwest and Southeast Australian Subregions, and the southern boundary of the Sino-Japanese Subregion, defined by the 20°C winter isotherm, extend outside the tropics (Fig. 1). In all cases there is a marked drop in species diversity outside the 20°C isotherm, with the appearance of one or more endemic species (Table 2). There are comparable subregions in the Western Atlantic. In the Eastern Atlantic and Eastern Pacific, where cold currents flow towards the equator, the north-south extent of the subregions is considerably less than in the Western Atlantic (Fig. 4) and Indo-West Pacific (Fig. 3). In addition, the paucity of species in the Eastern Atlantic does not permit the definition of

a possible subregion between Portugal and Cape Verde on the western tip of Africa.

Within the tropics, the less obvious limits — ocean currents, oceanic deeps, coastal geography — appear to be responsible for most of the discontinuities in penaeid distribution. Examples of how these barriers may operate in the Tropical Australian Subregion, which is apparently contiguous with the Indo-Malaysian Subregion, are described below and shown in Fig. 5. (The well-known water barriers of Wallacea that separate the terrestrial floras and faunas of Australia–New Guinea from southeast Asia are due to long-term movements of the tectonic plate [see review by Whitmore, 1981]; these barriers are not relevant to marine faunas with dispersive planktonic larvae.)

The Indo-Malaysian penaeid fauna attenuates along the north coast of New Guinea from west to east. In eastern New Guinea and the Solomon Islands, only 17 species, four of which are deep-sea, are common to the Indo-Malaysian Subregion, which contains 84 species. All of the 13 shallow-water species are wide-ranging: *Penaeus* spp. (7); *Metapenaeus* spp. (4); *Heteropeneus longimanus*; *Trachypenaeopsis richtersi*. The New Guinea Trench runs close to the steep mid-northern coast of New Guinea, resulting in a very narrow continental shelf (Fig. 5). Further to the east the end of the New Britain Trench comes close inshore. Except for the Sepik River, there are no major rivers along this coast and no extensive marine estuaries. The westward Equatorial Current flows close inshore for most of the year (Lindström *et al.*, 1987). The southeast coast of New Guinea is similar geographically to the north coast, but has an along-shore eastward current (CSIRO, unpubl.), which thus discourages westward migration of Penaeidae (such as *Metapenaeus affinis* and *M. anchistus*) from the eastern end of New Guinea towards Tropical Australia.

To the northwest of Australia the Java Trench extends along southern Indonesia, reaching in the east, past the island of Sumba; deep water

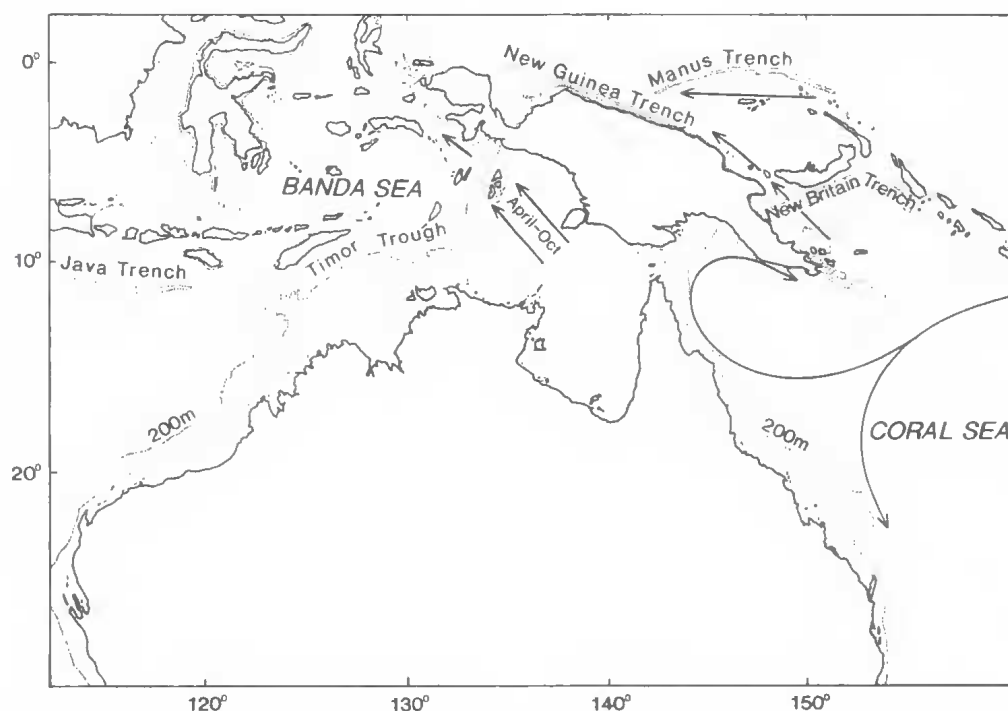


FIG. 5. Geographical features that tend to isolate the Tropical Australian Subregion from the Indo-Malaysian Subregion. Arrows indicate surface currents.

continues to the northeast as the Timor Trough, followed by the Aru Basin, coming close inshore at the neck of New Guinea (Fig. 5). Here the continental shelf is very narrow, which probably inhibits coast-wise migration of penaeids. The Banda and Aru Basins are fed by southerly inflows from the Pacific Ocean and this water then flows southwesterly through the Timor Trench (Van Aken *et al.*, 1988; Postma and Mook, 1988). Thus the net flow of intermediate and deep water is towards the Indian Ocean. In addition, from April to October the southeasterly trade winds produce a northwesterly shallow-water flow, which appears to cause upwelling and lower water temperatures (Fleminger, 1986). This cold water then joins the surface currents flowing to the northwest, carrying any penaeid larvae away from the extensive shallow coastal regions of southern New Guinea and Australia.

The effects of the November–March monsoon season on shallow-water movements do not appear to have been documented for this area. In open waters the winds tend to be northwesterly during this period, which would enhance migration of penaeid larvae towards Australia. But the

discontinuity between Indo-Malaysian and Tropical Australia faunas indicates that some kind of year-round barrier exists. (This barrier is, of course, only partial; there are many species common to both subregions.) The western end of New Guinea is geographically complex, with mountain ranges from 1000 m to over 4000 m high. Winds originating in the north-northwest and flowing across the neck of New Guinea (about 1000 m high), could be deflected by the much higher mountains in the east, resulting in local southerly, or even south-westerly winds crossing the south coast. Such winds would probably be cool and could produce further in-shore upwelling. Also, Fleminger (1986) reviewed evidence that, during the Pleistocene glaciation, water temperatures in this region may have been unusually cool for the tropics, due to cool prevailing winds and upwelling; this cooling may have acted as a barrier to tropical stenotherms. Dall *et al.* (1990) point out that during the maximum of the Quaternary Glacial Period the lowered sea levels would have resulted in most of the sea between New Guinea and Australia becoming dry land. There would have been a steep coast, with virtually no shallow

TABLE 4. Apparent sibling species in the temperate subregions of southern continents and their more widely-ranging, usually tropical 'parent' species.

Subregion	Sibling species	Parent species
Southeast South America	<i>Penaeus paulensis</i>	? <i>P. aztecus</i>
South Africa	<i>Metapenaeopsis scotti</i>	? <i>M. philippii</i>
Southwest Australia	<i>M. insona</i>	<i>M. quinquedentata</i>
	<i>M. fusca</i>	<i>M. barbata</i>
	<i>M. lindae</i>	? <i>M. acclivis</i>
Southeast Australia	<i>M. insona</i>	<i>M. quinquedentata</i>
	<i>Metapenaeus bennettiae</i>	<i>M. moyebi</i>
	<i>Penaeus plebejus</i>	<i>P. latisulcatus</i>

water, connecting the two subregions, probably eliminating the migration of shallow-water penaeids during the last glacial period. The migration of penaeids towards the northern Australian area from Indonesia, appears, therefore, to have been restricted since the Pleistocene.

The northwest coast of Australia, which is arid, with hypersaline inshore waters also appears to be unfavourable to penaeid colonisation. Of 36 shallow-water species in northern and north-eastern Australia, only 18 also occur in the far northwest of the continent.

SOUTHERN HEMISPHERE ENDEMISM IN THE PENAEIDAE

The Northern Hemisphere has only one subregion (the Sino-Japanese) outside the tropics that includes endemic species, whereas in the Southern Hemisphere the South African, Southwest Australian, Southeast Australian and the Southeast South American Subregions all contain endemic species (Tables 2, 3). Some of these are closely similar to more widely distributed tropical species and may be sibling species (Table 4), but there are also three Southern Hemisphere species which do not have any close affinities. *Metapenaeus macleayi* in Southeast Australia is distinctive within its genus, but *Macropetasma africanus* in South Africa and *Artemesia longinaris* in Southeast South America are more exceptional. Both are monospecific genera, they are quite different from one another and from other genera, both fossil and present, of the Penaeidae. *Artemesia* and, to a lesser extent *Macropetasma* inhabit waters cooler than is usual for the Penaeidae.

Newman and Foster (1987) conclude that endemism of barnacles in the Southern Hemisphere is due to:

1. Extinction processes (either at low latitudes or of Northern Hemisphere counterparts).

2. Evolution of long indigenous taxa.

Unlike barnacles, the Penaeidae have a very poor fossil record and extinction hypotheses cannot be tested, but as a predominantly tropical group, extinction within the tropics is probably less likely than in more widely ranging groups. There do not appear to be any clear examples of amphitropicality in the Penaeidae. There are Northern or Southern Hemisphere endemic species, but no matching pairs of species, nor are there any species with a clear break in distribution in the tropics. *P. aztecus* and *P. paulensis* in the Western Atlantic may be amphitropical species, but the affinities of the Western Atlantic complex of grooved *Penaeus* species needs further research. *Metapenaeopsis acclivis* and *M. lindae* in the Indo-West Pacific may also be amphitropical, but there are significant morphological differences between them and this genus also needs further research. The most usual situation is for a northern or southern endemic to have a closely related species, which could be a parent, in the adjacent tropics (Table 4).

The uniqueness of *Macropetasma* and *Artemesia* suggests that they could be relict species from much more widely ranging populations. Dall *et al.* (1990) examine the possibility that they could be Gondwana relicts, but find this hypothesis to be untenable. *Macropetasma* is unique among the Penaeidae in possessing photophores; *Artemesia* superficially resembles some deep-water Penaeoidea. Thus they could be relicts of a deep-water, possibly amphitropical group, but there are no similar extant deep-sea genera to support this hypothesis and wholesale extinction would need to be invoked. Alternatively, they could have been once widely distributed in the cooler conditions of the Miocene and subsequently became extinct in the tropics (Valen-

tine, 1984). Although plausible, in the absence of any supporting data, this hypothesis must also remain pure conjecture.

However, the rate of evolution of penaeid genera, discussed earlier, suggests that *Macropetasma* and *Artemesia* could well have evolved since the middle Tertiary. (*Protrachypene* is another unique monospecific genus in the Eastern Pacific Region that has presumably evolved since the Caribbean fauna became separated from that of the Eastern Pacific in the Miocene). *Metapenaeus macleayi* and the sibling species listed in Table 4 could have evolved more recently. Dall *et al.* (1990) estimate from genetical evidence that the sibling species *Metapenaeus bennettiae* and *Penaeus plebejus* in Southeast Australia probably evolved in the last two million years. This area was separated geographically from the rest of the Indo-West Pacific during the last glacial epoch. The cold-adapted *Penaeus chinensis* must also have evolved from the closely similar and geologically ancient *P. merguensis* - *indicus* group since the last glacial epoch; the shallow Pohai and Yellow Seas would have been isolated lakes or dry land at the height of this period. Dall *et al.* (1990) point out that the lowering of sea-levels in the late Tertiary and Quaternary would have produced extensive land bridges in former shallow seas; these would have acted as effective barriers and thus enhanced penaeid speciation during this period. The limited range of many species of Penaeidae also point to such processes in the evolution of the family.

In summary, in the absence of fossil evidence to the contrary, evolution of pre-existing taxa can account for the endemism of the Southern Hemisphere Penaeidae.

Macropetasma and *Artemesia* may be exceptions and are relicts of widely-ranging Miocene populations, but further evidence is needed to support this hypothesis.

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